

Structure and Function of the Ear and Auditory Nervous System

by Merle Lawrence*

The transduction from sound vibrations to a nerve ending stimulus takes place in the organ of Corti. This process, resulting from fluid particle movement of a magnitude equivalent to the dimensions of the electron cloud around an atom, involves more than a simple deformation of the sensory cell.

The fluid environment of these cells must be such that it provides sufficient oxygen and nutrients for the cells' survival and at the same time maintains a condition to enhance the biophysical process. The spiral capillaries beneath the tunnel of Corti furnish the metabolites for the Cortilymph surrounding the sensory cells. The capillaries of the stria vascularis provide this structure, an organ in its own right, so that it can maintain the high potassium concentration and positive potential of endolymph which are necessary for the transduction process.

The stria vascularis itself and its blood supply and the sensory cells and their blood supply are all vulnerable to attack by various toxic agents, thus altering the homeostatic condition and resulting in a hearing loss.

Of the two basic peripheral processes of hearing, sound conduction and sound conversion to a coded nerve impulse, certainly the latter is the more complicated and mysterious. It is here that an extremely minute molecular disturbance is analyzed and a stimulus to a diverse network of fine unmyelinated nerve fibers is produced. To maintain a living organ in a condition to accomplish this feat requires a most delicate balance of the chemical environment. The arrangement is such that there is a fluid system within a fluid system (Fig. 1), and the mechanisms of chemical exchange between these two are far from understood.

The Labyrinths

The bony labyrinth within the petrous portion of the temporal bone is filled with perilymph which is connected with the cerebral spinal fluid (CSF) by the cochlear aqueduct. The patency of this duct varies among the species and even in different stages of life in man. During fetal life and in the newborn human this aqueduct is wide open, but in

the adult it becomes quite narrow and passes through a long bony channel.

At the labyrinthine end, the cochlear aqueduct opens into the scala tympani of the inner ear in the

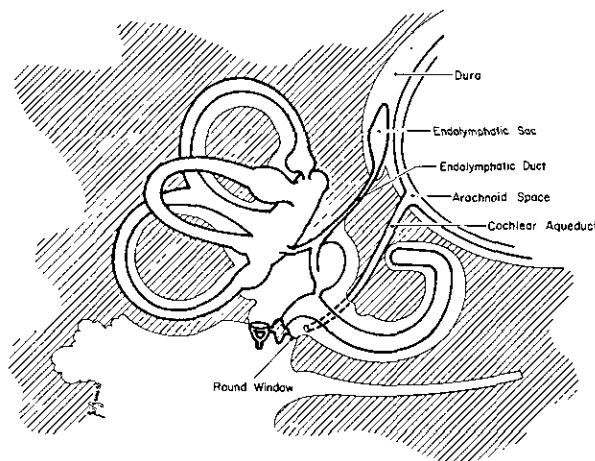


FIGURE 1. The labyrinths of the ear. The bony labyrinth is filled with perilymph which differs slightly from the cerebrospinal fluid to which it is connected. The endolymphatic system surrounded by perilymph is a closed but not stagnant system.

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region of the round window beneath the basilar membrane. As the scala tympani, comprising the space between the basilar membrane and the bony wall of the otic capsule, twists with the spirals of the cochlea, it meets, at the apex through an opening, the helicotrema, with the scala vestibuli. The perilymph continues to fill this scala as it winds back down the turns of the cochlea between the bony separation between turns and Reissner's membrane. The bony labyrinth of the scala vestibuli widens at the base to surround the membranous utricle and saccule and then continues around the semicircular canals. The footplate of the stapes borders this enlarged vestibule of perilymph and conveys its minute motion to the endolymph through the perilymph and Reissner's membrane.

Because the cochlear aqueduct enters the perilymphatic channels at one end of the bony labyrinth it seems unlikely that when everything is normal CSF flows into the inner ear. More than likely, and there is evidence for this, perilymph is produced within the inner ear and is slowly absorbed into the CSF system.

More sodium and protein are added to perilymph somewhere within the perilymphatic system. In the region of the spiral ligament above Reissner's membrane (Fig. 2), there is a capillary network

that may well be responsible for providing perilymph with those chemical characteristics that make it different from CSF. The capillaries are close to the surface and are arranged in a way to suggest the formation of a plasma filtrate.

The endolymphatic fluid is a closed system separated from perilymph by Reissner's membrane, basilar membrane, and the membranous walls of the utricle, saccule, and semicircular canals. Continuous with the duct connecting the utricle and saccule midway between the cochlear and vestibular complexes is the endolymphatic duct which, like the perilymphatic aqueduct, passes through bone to end in a closed sac within the folds of the dura. Like perilymph, endolymph is not a stagnant pool. The fluid is generated and its ionic contents controlled within the membranous labyrinth, all the while slowly moving in the direction of the endolymphatic duct to be absorbed in the endolymphatic sac.

The blood supply to the membranous labyrinth is separate from that of the otic capsule. The cochlear artery, entering the internal auditory meatus is a terminal branch of the vertebral-basilar artery complex. After entering the modiolus the artery coils around the nerve, giving off branching arterioles which supply capillaries to the various parts of the labyrinthine structures.

The Stria Vascularis

In a spiral groove (Fig. 2) of the otic capsule around the coils of the cochlea is the spiral ligament. This forms one boundary of the triangular-shaped scala media. Along the surface facing the endolymph is a specialized structure, the stria vascularis, that provides for the peculiar characteristics of the endolymph.

The stria vascularis is a unique structure with specialized cells. These have been described mostly in guinea pig from observations made by both light and electron microscopy. Kimura and Schuknecht (1) describe, in humans, the ultrastructure of the three types of cells making up the stria vascularis. The cells on the endolymphatic surface are the marginal or dark cells whose nuclei are close to this surface. On the opposite surface of these cells the membrane is deeply corrugated, interlocking with the cells of the intermediate and basal cells. The luminal surface of the marginal cells shows varying numbers of microvilli and pinocytotic invaginations. An extensive network of tubules filled with a diffuse substance lies close to the luminal surface, and marginal cells adjacent to each other are interlocked with numerous infoldings.

The intermediate or light cells are fewer in number than the marginal cells with which they

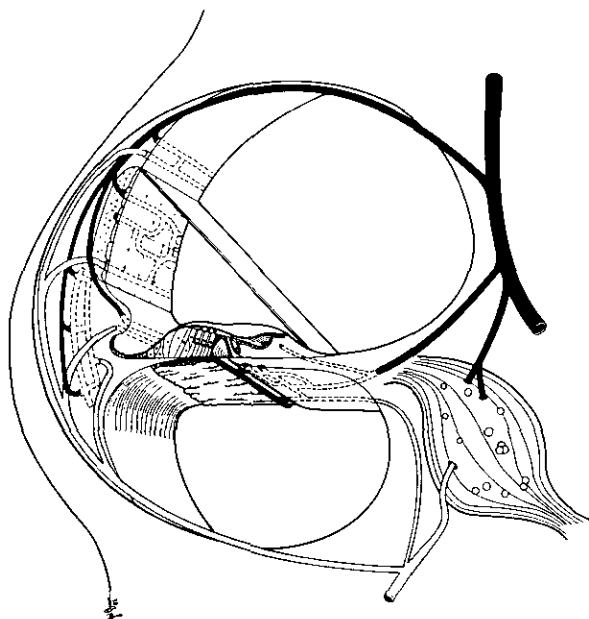


FIGURE 2. The cochlear duct in cross section shows the various capillary areas referred to in the text. The region about which something is known are (a) the capillaries in the spiral ligament above Reissner's membrane, (b) the stria vascularis, (c) the spiral capillaries beneath the tunnel of Corti.

interlock. They contain a rather large number of mitochondria.

The basal cells lie next to the spiral ligament. They are flat and long with cell processes that extend a short distance toward the marginal cells.

Jahnke (2), using freeze-fracture techniques in the guinea pig, adds that the marginal cells appear to provide a barrier between the endolymphatic space and the intracellular spaces. But these spaces are very tightly sealed to the spiral ligament so that the spaces appear to make up a compartment.

The capillaries of this area enter through the basal cell layer and pass among the intermediate and marginal cells. Smooth muscle cells and neural elements are absent in these capillaries whose endothelial cell walls are extremely thin but not fenestrated.

The stria vascularis whose marginal cells lie

between the capillaries and endolymph is responsible for maintaining the high potassium content of the endolymph. Along with this high potassium, endolymph has a positive electrical (approximately +80 mV) with respect to perilymph. The source of this potential has been localized to the stria vascularis (3) and is believed to be the result of the combined effect of an electrogenic pump and a potassium diffusion potential (4): the electrogenic component generating +100 mV and the potassium diffusion potential accounting for -20 mV. It is further theorized that the pump is located in the membrane of the marginal cells facing the endolymph.

It appears then that the stria vascularis is an organ in its own right. It has a high rate of metabolism and requires oxygen from its own capillaries. The oxygen that can be measured by an electrode in the scala media diffuses out from the stria.

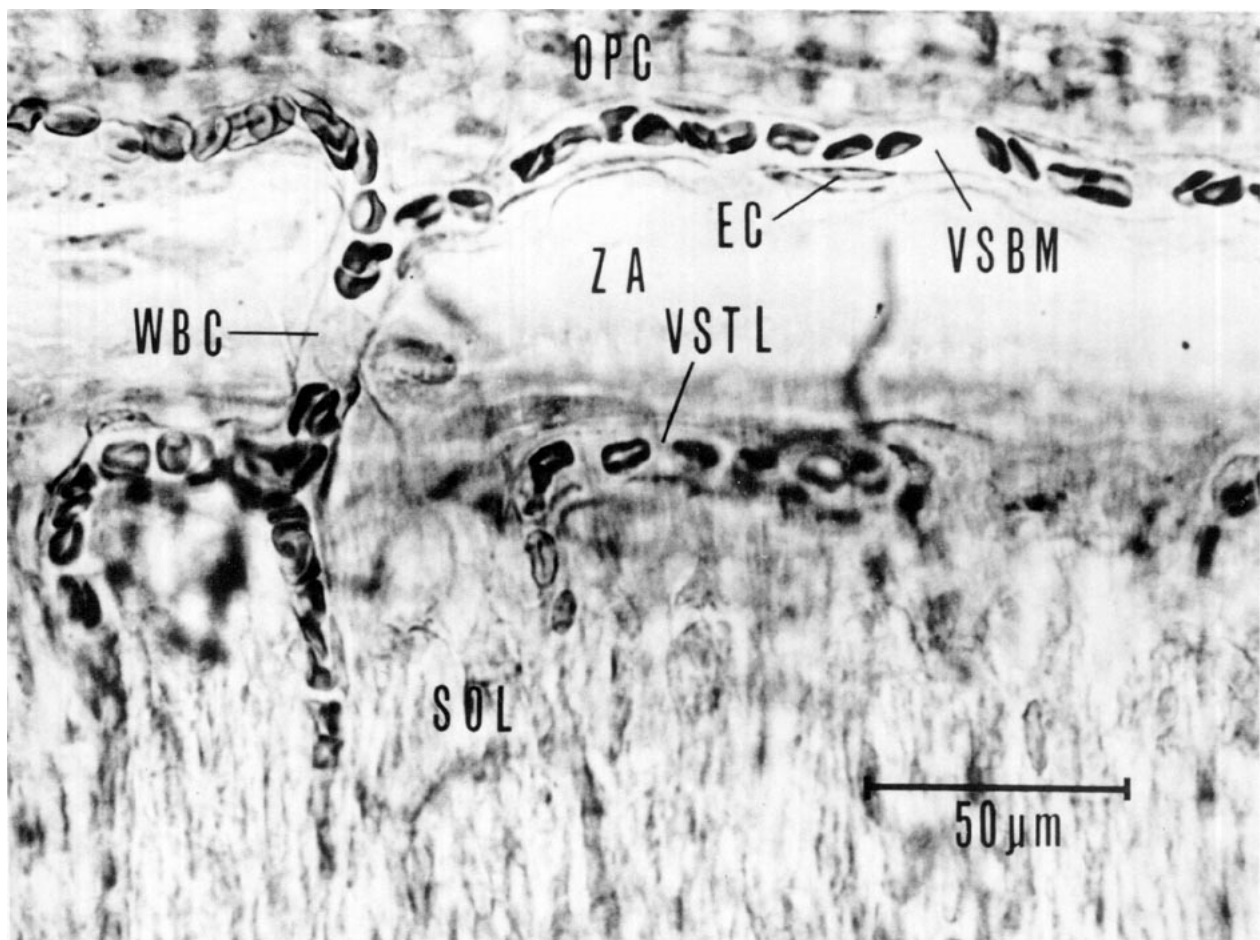


FIGURE 3. A view beneath the tunnel of Corti from the scala tympani side. The region beneath the tunnel is much thinner than the rest of the basilar membrane; (ZA) zona arcuata (area beneath the tunnel); (EC) endothelial cell of capillary; (OPC) outer pillar cell; (SOL) spiral osseous lamina; (VSBM) vessel of the basilar membrane; (VSTL) vessel of the tympanic lip. (WBC) white blood cell.

The Sensory Cells

The sensory cells of the organ of Corti are protected from endolymph and get their oxygen and nutrients from the spiral vessels.

The capillaries of the osseous spiral lamina emerge beneath the organ of Corti to form two parallel systems lying beneath the feet of the pillar cells, thus bordering the tunnel (Fig. 3). The distance between these capillaries and the hair cells is generally less than 50 μm , while the distance from capillary to tunnel fluid is only a few microns (5). The basilar membrane, the organ of Corti, and these capillaries are so situated that fluid exchange is facilitated. The feet of the inner pillar cells rest on the edge of the spiral lamina between the habenula perforata and the attachment of the basilar membrane. From this attachment to a point beneath the outer pillars there is only a thin fibrous layer separating the fluid spaces of the tunnel and the lamella cells on the scala tympani side.

As described, perilymph fills the scala tympani beneath the basilar membrane and easily passes through the thin area of the basilar membrane, named by Corti as the zona arcuata, between the pillars. This Cortilymph (6) within the organ of Corti differs from perilymph by the oxygen and nutrients that diffuse from the spiral capillaries.

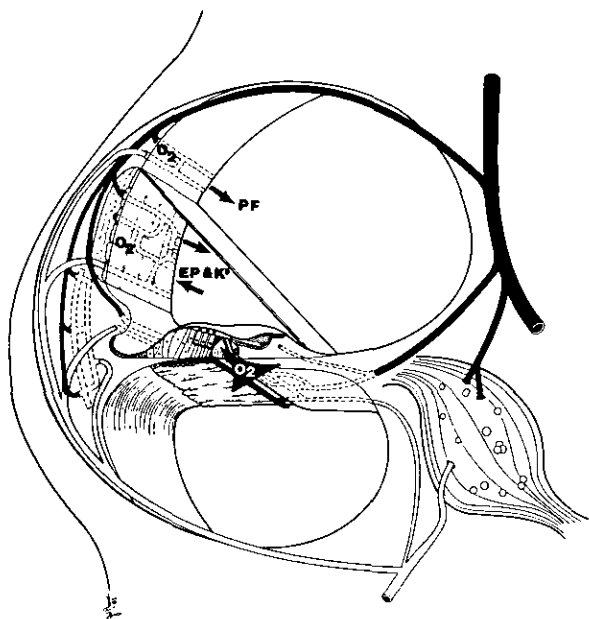


FIGURE 4. Functions of capillary areas vulnerable to attack by toxins: (PF) plasma filtrate providing perilymph with its chemical constituents; (EP and K^+) endolymphatic potential and high potassium controlled by the stria vascularis; (O_2) the oxygen sources for the areas maintaining microhomeostasis.

Several lines of evidence have indicated the role of the spiral vessels in the maintenance of Cortilymph. Vosteen (7) reviewed a number of experiments that indicate the spiral vessels as the main source of oxygen for the sensory cells. In other studies, direct measures of oxygen availability were made simultaneously (8) in the tunnel fluid and endolymph as the animal was made anoxic by shut-off of respiratory air. Oxygen concentration in the tunnel changed rapidly with the anoxic condition of the animal whereas the oxygen concentration of the endolymph responded much more slowly. Apparently the spiral vessels provide the oxygen directly to the sensory cells.

Adequate function of these sensory cells, the *sine qua non* of hearing, requires more than a sufficient oxygen supply. Even though the sensory cells are protected from endolymph, the positive endolymphatic potential plays an important role. So the capillary blood supply to both the tunnel of Corti and the stria vascularis is most important (Fig. 4). However, the oxygen released by the stria vascularis capillaries is utilized by the stria vascularis itself (9, 10) and is not a supply for the sensory cells.

Areas of Vulnerability

There are then several capillary areas and transport functions that can be affected by toxic agents. We have reported (11) an absence of blood cells in both the stria vascularis and in the spiral vessels following an acoustic overstimulation in the guinea pig. Hawkins (12) has reported that for adequate dosages of both quinine (quinine dihydrochloride) and salicylates (sodium salicylate) there results a partial occlusion of the spiral capillaries by the swollen endothelial cells which block the passage of blood cells.

Pike and Bosher (13) have shown that intravenous furosemide in guinea pigs produces ultrastructural abnormalities in the marginal cells of the stria vascularis with shrinkage of intermediate cells and enlargement of the intercellular spaces. These changes are correlated with changes in the ion-transporting mechanism of the stria (14).

Ototoxic drugs may also affect the capillaries above Reissner's membrane (15), and changes in the ionic content of the endolymph may affect the tectorial membrane, thus changing the adequate performance of the organ of Corti itself (16).

It is apparent, then, that both morphology and function of the ear and its physiological processes are subject to changes resulting in alterations of the microhomeostatic conditions of the organ of Corti. Some drugs, such as the salicylates, will produce a

partial hearing loss that may exist as long as the drug is taken but when stopped, hearing returns to normal. Of the physiological processes just described one might ask which ones are able to function at "half normal." Perhaps all of them, but most ototoxic effects from the antibiotics and diuretics seem to be permanent. However, the endolymphatic potential upon which adequate function of the organ of Corti seems to depend can be reduced and maintained at lowered levels by reduction in blood oxygen.

Experiments (17) have shown that the reduced endocochlear potential from partial anoxia can be maintained over relatively long periods of time. Perhaps such an effect can account for the reversible hearing loss seen in some deafnesses resulting from toxins.

This brief outline of the morphology and possible physiological functions of capillary areas and cell groups covers only in a very sketchy way the processes that we know about. Why certain toxins have an affinity for the ear may be related to the lack of replaceable cell groups and the poor redundancy of the blood supply.

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